Considerations on Paleozoic Polyplacophora including the description of *Plasiochiton curiosus* n. gen. and sp.

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Abstract: Numerous occurrences of undescribed Paleozoic polyplacophorans have been located, and new taxa of Silurian, Mississippian, and Permain specimens have been recently described. Problems commonly exist in classifying isolated plates at the species level. Sizes and patterns of aesthetes show some differences in plate microstructure between Paleozoic and modern taxa. Recently proposed classifications indicate differences of opinion concerning relationships and inclusion of non-polyplacophoran taxa. A possible, but incomplete, phylogenetic scheme at the family level is presented. *Plasiochiton curiosus* n. gen. and sp. is described from the Devonian of Pennsylvania.

Key Words: Mollusca, Polyplacophora, Paleozoic, classification, phylogeny

Paleozoic polyplacophorans are not as rare stratigraphically and numerically as one might be led to believe from the published literature, largely as a result of collections remaining undescribed. Collections by the author and associates in Pennsylvanian age strata of the Appalachian basin have found over 50 localities containing one to hundreds of plates of polyplacophorans. In many cases, specimens are placed in repositories with little or no reference to their existence. Inquiries to museums, universities, and individuals commonly turn up specimens, many of which are important in our understanding of the classificiation and phylogeny of the class. It is likely that individuals processing samples for ostracodes and foraminifers, have found, but did not recognize polyplacophoran plates, especially if the plates were fragmented. It is important to illustrate and specify in the literature the location of specimens to make known their existence.

Illustrated specimens herein are in the repositories of the National Museum of Natural History (USNM), Ohio University Zoological Collections (OUZC), and New York State Museum (NYSM).

RECENT STUDIES

Since I began work on this study a number of undescribed specimens have been found. These include: two Ordovician plates of *Gotlandochiton* from Minnesota and two plates of *Chelodes* from the Ordovician of Alabama (Fig. 1); Silurian specimens from California containing new species of *Paleochiton* and *Thairoplax*, only the second known Silurian fauna from North America (Hoare, 2000a); an articulated partial specimen of a new genus from the Devonian of Pennsylvania (described herein); Devonian plates of *Arcochiton*? and *Gotlandochiton* and Mississippian plates of *Gryphochiton* from Australia (Hoare and Cook, 2000); an abundant Mississippian fauna from Iowa containing new species of *Gryphochiton* and *Euleptochiton* and three new genera (Hoare, 2000c), a fauna quite different from that of the Salem Limestone in Indiana described by Kues (1978); two Mississippian plates of *Gryphochiton* from Kentucky, an undetermined Mississippian plate from Morocco, and a Permian plate of *Cymatochiton* from Sicily (Fig. 2); and Permian specimens from Argentina (Hoare and Sabattini, 2000), Malaysia (Hoare, 2000b), and Oregon (Hanger *et al.*, 2000), containing a number of new genera and species. A new Devonian genus from Germany and a new Permian genus from the U. S. are in press (Hoare, 2001). The Malaysian specimens are particulary interesting in their very large size with thick shell material. Recent studies by Cherns (1998a, b) have added significantly to our knowledge of Silurian polyplacophorans. Undoubtedly there are still numerous taxa that have not been found or described.

A significant collection of Lower Carboniferous specimens from Belgium has also been discovered. A study of this collection plus known collections at Harvard University and the Smithsonian Institution will allow a

Fig. 1. 1-8, *Gotlandochiton* sp., Oneata Fm. (Ordovician), Minnesota. 1-4, dorsal, ventral, anterior, and right lateral views of a tail plate, USNM 501824 (bar scale = 1 cm); 5-8, dorsal, posterior, ventral, and right lateral views of an intermediate plate, USNM 501825. 9-15, *Chelodes* sp., Odenville Fm. (Ordovician), Alabama. 9-12, dorsal, ventral, anterior, and left lateral views of a tail plate, USNM 501826; 13-15, posterior, right lateral, and dorsal views of an intermediate plate, USNM 501827 (bar scale = 1 cm).

review of their taxonomic relationships which, as described and illustrated by de Koninck (1842, 1883), Münster (1839, 1843), and de Ryckholt (1845, 1852), appear to contain a number of synonymous taxa.

PROBLEMS

The study of fossil polyplacophorans is challenging because the dorsal plates usually become disarticulated and are most commonly found as isolated entities. Complete articulated specimens are rare, although the occurrence of numerous specimens of *Glaphurochiton concinnus* (Richardson, 1956) in the Pennsylvanian Francis Creek Shale in Illinois is a notable exception. These specimens also show the presence of radula, girdle, and spines (Yochelson and Richardson, 1979). Incomplete articulated specimens are also helpful in determining the correct association of isolated plates.

Isolated plates, when described and named, have led to taxonomic confusion. As an example, Dunlop (1922), by careful collecting at one locality, was able to show that *Chiton cordatus* Kirkby, 1859, a head plate, *C. armstrongianus* Etheridge, 1882, an intermediate plate, and *C. gemmatus* Kirkby, 1862, a tail plate, were all parts of the same species, *C. cordatus* Kirkby, 1859 [=*Lekiskochiton cordatus* (Kirkby, 1859)]. Because intermediate plates are usually more commonly found, a number of species have been erected on the basis of a single plate. Tail plates of most Paleozoic taxa are more diagnostic than head or intermediate plates and distinction between genera and species can often be made on these plates alone. Tail plates also provide much of the ontogenetic evidence of a taxon (Fig. 3).

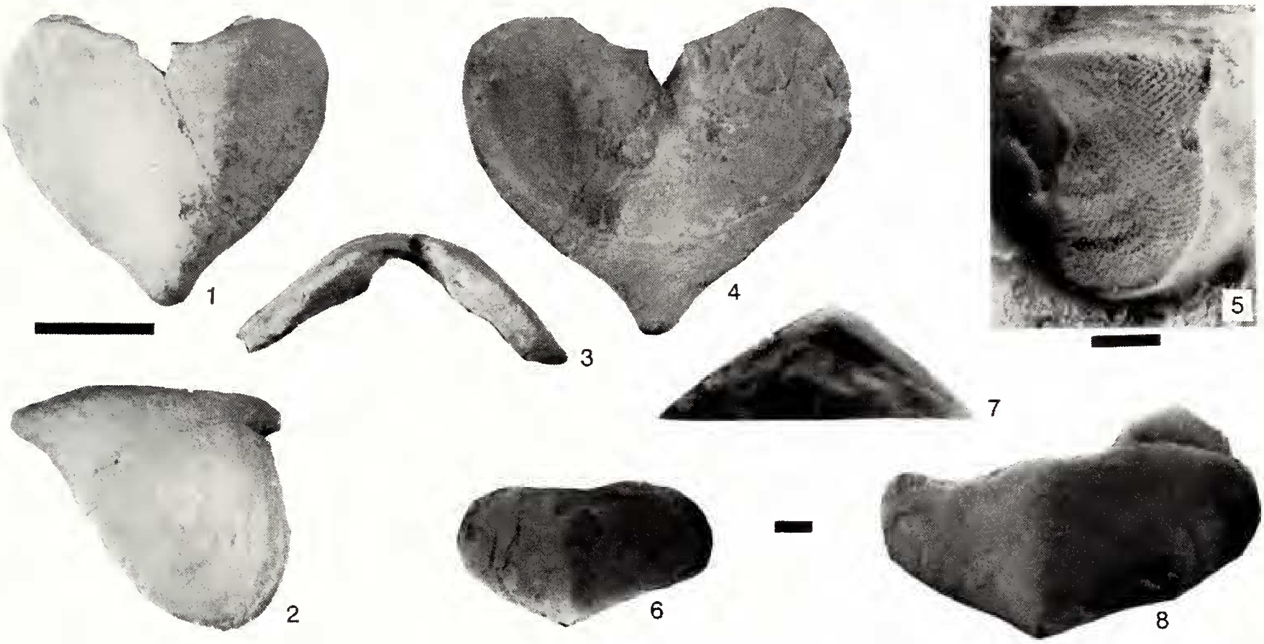

Fig. 2. 1-4, *Cymatochiton* sp., Socio Ls. (Permian), Sicily. Dorsal, right lateral, anterior, and ventral views of an intermediate plate, USNM acc. No. 179,820 (bar scale = 1 cm). Note large apical area on ventral surface. 5, Undetermined sp., Mississippian formation, Morocco. Oblique right lateral view of an intermediate plate, OUZC 1633 (bar scale = 1 mm). 6-8, *Gryphochiton parvus* (Stevens), Tribune Ls. (Mississippian), Ky. Dorsal and posterior views of an intermediate plate, USNM 508371, and a dorsal view of an intermediate plate, USNM 508372, (bar scale = 1 mm).

PLATE MICROSTRUCTURE

Previous studies of plate microstructure (*e. g.* von Knorre, 1925; Bergenhayn, 1930; Haas, 1972) have normally been made by cutting the plates vertically showing disposition of shell layers and the occasional aesthete exposed in the section. Such sections do not show the pattern of the aesthetes. In cutting a piece of a plate parallel to and just below the dorsal surface of the tegmentum the size, pattern, and distribution of the aesthetes can be determined. Haas (1972) cut Recent material parallel to the plate surface.

Specimens of nine species representing six genera of Mississippian and Pennsylvanian taxa were sectioned. Preservation of the aesthetes ranged from poor to excellent (Fig. 4) and measurements of diameters and spacing were made. Several preliminary conclusions were reached:

1. No size distinction for micraesthetes and megaesthetes was present in any specimen;
2. No pattern of micraesthetes encircling megaesthetes or any other circular pattern was seen. Such patterns must have developed post-Paleozoic;
3. For coarser surface ornamentation of pustules, the diameter of the aesthetes was larger, with one aesthete per pustule;
4. Aesthete diameter ranged in size from 19.3 μm to 31.2 μm in the specimens;
5. Several specimens showed aesthetes centered in polygonal structures. Whether this is an artifact of preservation or a structure related to plate development is unknown.

CLASSIFICATION

A number of multiplated organisms other than polyplacophorans are known to occur in the Paleozoic. The opportunity to study specimens of several of these taxa has led the author to reevaluate what should be or should not be included in the Polyplacophora. Some of these (*e. g. Diadeloplax, Strobilepis, Aenigmatectus*) from the upper Paleozoic have some characteristics in common with polyplacophorans including mucros on tail plates, insertion plates, and apical areas. However, the shapes, arrangements, and ornamentation of the plates are usually quite different and the canal system in the plates is different from the aesthetes in polyplacophorans (Hoare and Mapes, 1995, 1996).

Bischoff (1981) included Ordovician-Silurian phosphatic multiplated organisms from Australia in the Polyplacophora. Besides being of a different composition these plates show structural differences from polyplacophorans such as plate growth patterns, microstructure, and supposed insertion plates. Yu (1984, 1987) has illustrated and described a number of multiplated taxa from the

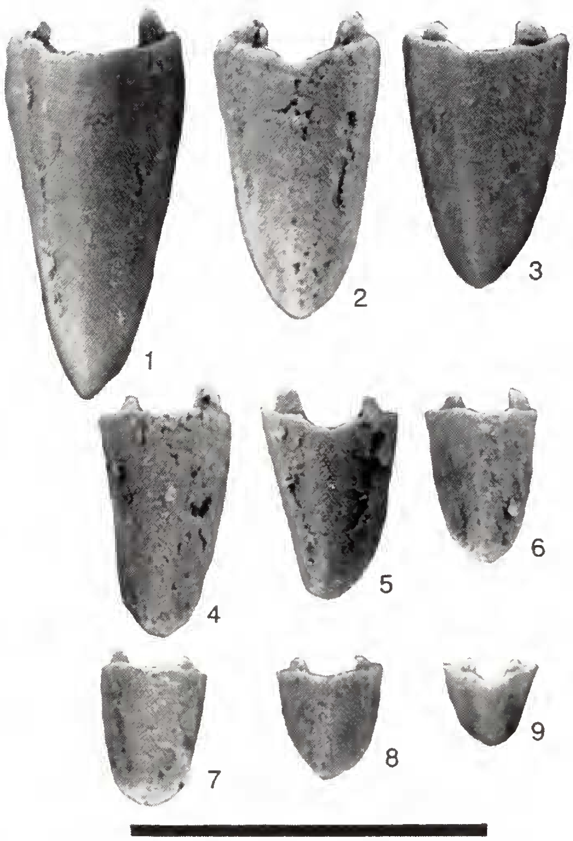

Fig. 3. *Acutichiton allynsmithi* Hoare, Mapes, and Atwater. Gene Autry Fm. (Pennsylvanian), Oklahoma. 1-9, dorsal views of a series of tail plates showing increase in size and change in shape during ontogeny, OUZC 1621-1629 (bar scale = 0.5 cm).

Lower Cambrian of China placing them in the Polyplacophora under five new families. These are small specimens, mostly less than 0.5 mm in width. Sirenko (1997) questioned the inclusion of these in the Polyplacophora, a conclusion with which I agree.

The family Septemchitonidae Bergenhayn, 1955, contains multiplated organisms that developed plates that curve inward ventrally almost closing off the area for the position of the foot as illustrated by Dzik (1994, fig. 29). These plates are totally unlike polyplacophoran plate shape and the family is here omitted from the class. It is expected that many other types of multiplated organisms will eventually be discovered in Paleozoic strata.

Most recently, Sirenko's (1997) classification of polyplacophorans recognized four orders, five suborders, and 14 families, including one new family, in the Paleozoic. Changes from his scheme suggested here (Fig. 5) include the recognition of the family Matthevidae Walcott (1886) in place of Chelodidae Bergenhayn (1943), the elimination of the family Septemchitonidae Bergenhayn (1955), and the addition of the family Choriplacidae Cotton and Weeding (1939). The latter is included based upon the new Devonian genus and species described herein, which has many characters comparable to the genus *Choriplax* Pilsbry, 1894.

PHYLOGENY

As with the classification, there are more questions than answers related to the phylogeny of the Polyplacophora at this time. This situation is true even to the extent of determining the origin of the class and relationship with other mollusks. It is not the purpose of this study to discuss the origin of the phylum or that of the polyplacophorans. However, polyplacophorans are so different from other mollusks in terms of their skeletal and anatomical structures that it seems likely that the phylum is polyphyletic.

Yu (1989) proposed a multiplated ancestral stem leading to the polyplacophorans from which other molluscan classes developed. The Polyplacophora undoubtedly developed from a segmented ancestral form but it seems very unlikely that the single or double plated classes of other mollusks arose from a similar ancestor (Runnegar and Pojeta, 1974; Pojeta, 1980).

Figure 5 shows a possible phylogenetic relationship at the family level. It is based in part on the classification given by Sirenko (1997). There will be additional families added to this scheme based upon the studies of Cherns (1998a, b) in the Silurian, possibly in the Permian by the author, and by the discovery of additional specimens in the future.

SYSTEMATICS

Class Polyplacophora de Blainville, 1816
Order Neoloricata Bergenhayn, 1955
Suborder Lepidopleurina Thiele, 1910
Family Choriplacidae Cotton and Weeding, 1939
Genus *Plasiochiton* n. gen.

Type species. *Plasiochiton curiosus* n. sp.

Diagnosis. Intermediate plates subrectangular, wider than long, moderately arched, broadly convex; semicircular raised areas marked by concentric ridges on anterior jugal areas.

Description. See under *Plasiochiton curiosus* n. sp.

Discussion. This taxon is based upon a single incomplete articulated specimen. *Plasiochiton* differs from *Glyptochiton* de Koninck, 1883, in the shape of the plates and the shape and position of the raised jugal portion. The Recent genus *Choriplax* Pilsbry, 1894, is similar to *Plasiochiton* in its subrectangular plates with a raised and restricted tegmentum region located on the median portion

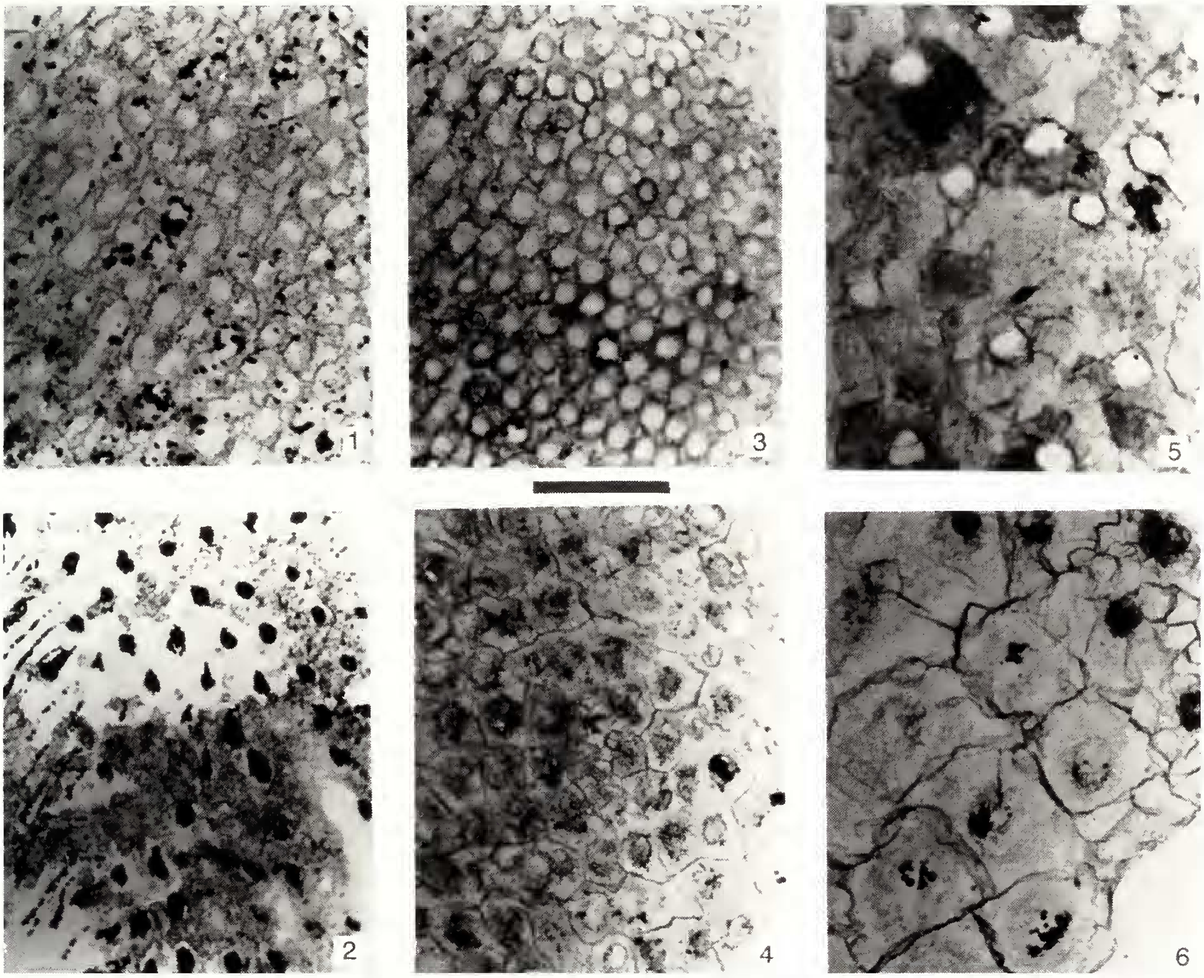

Fig. 4. Thin sections showing size and distribution of aesthetes on intermediate plates. 1, *Acutichiton pyramidalus* Hoare, Sturgeon, and Hoare, Vanport Ls., Ohio; 2, *Elachychiton juxaterminus* Hoare and Mapes, Imo Fm., Ark.; 3, *Euleptochiton spatulatus* (Hoare, Sturgeon, and Hoare), Vanport Ls., Ohio; 4, *Gryphochiton simplex* (Raymond), Vanport Ls., Ohio; 5-6, *Glaphurochiton carbonarius* (Stevens), Putnam Hill Sh. and Washingtonville Sh., Ohio, OUZC 1633-1638 (bar scale = 100 µm). Note the differences in size and distribution of the aesthetes and the polygonal structure in 4 and 6. (Sections prepared by B. R. Hoare).

of the intermediate plates. *Plasiochiton* is questionably assigned to the family Choriplacidae on this basis.

Occurrence. Known only from the type locality of *P. curiosus*, Devonian (Erian).

Etymology. Greek, *plasion*, oblong body.

Plasiochiton curiosus n. sp.

Fig. 6

Polyplacophoran Petzold, Clark, Makin, Owens, and Perry, 1992, p. 342, Fig. 1.

Diagnosis. As for the genus.

Description. Incomplete, articulated specimen of five plates preserved as mold of ventral surface; intermediate plates subrectangular, moderately arched, broadly convex, wider than long; posterior margins straight meeting lateral margins at right angles; anterior margin not observed; raised anterior jugal areas marked by concentric ridges in U-shaped pattern; raised area smaller towards posterior of specimen; shell material thin; head and tail plates unknown.

Measurements. Size of exposed specimen 17 mm long, 4 mm wide; exposed plates range from 1.8 to 2.5 mm in length and from 4.0 to 4.6 mm in width; estimated approximate total length 30 mm, total width 9.0 mm, and total height 4.0 mm.

Etymology. Latin, *curiosus*, odd, strange.

Type. Holotype, USNM 456242.

Type locality. Devonian Sherman Ridge Member of the Mahantango Formation exposed in an abandoned shale pit at the intersection of U.S. 11-15 and Pennsylvania 104, Perry Co., Pennsylvania, 40°36'52"N, 76°57'21"W, Millersburg 7.5 minute quadrangle.

Discussion. Devonian polyplacophorans are little known in

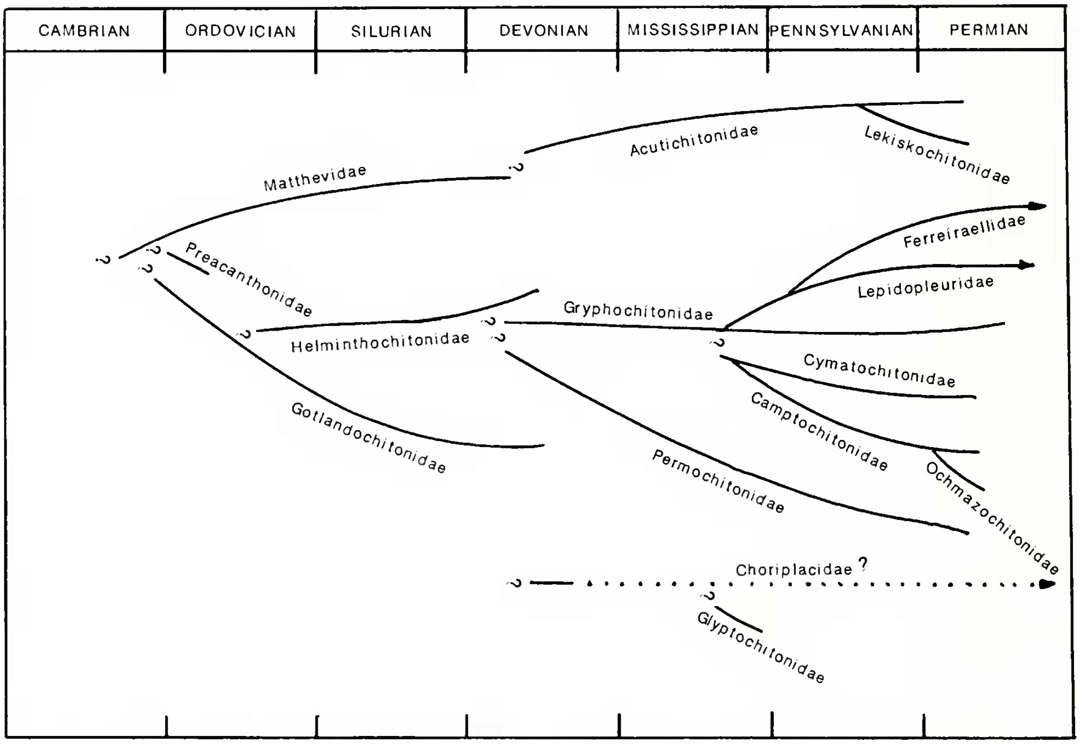

Fig. 5. A schematic phylogenetic diagram showing possible relationships at the family level.

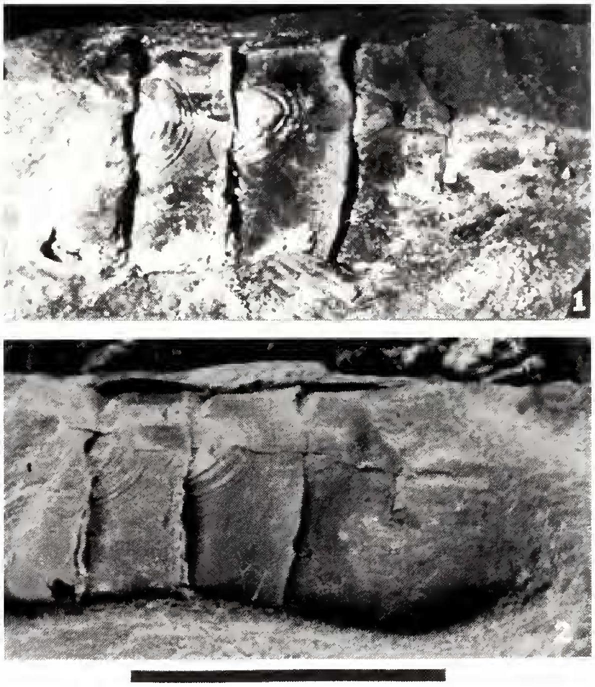

Fig. 6. *Plasiochiton curiosus* n. gen. and sp. 1, uncoated and 2, coated dorsally oblique views of a partial articulated ventral mold, Mahantango Fm. (Devonian), Pennsylvania, USNM 456242 (bar scale = 1 cm). Note the subrectangular shape of the plates and the medial anterior restriction of the tegmentum layer. (Fig. 1 from Petzold *et al.*, 1992, p. 342, published with the permission of the publisher and author).

North America and this specimen is important to our understanding of the development of the class in the Paleozoic. Unfortunately the shell material is lacking, but the mold is diagnostic in the shape of the plates and the semicircular structure on the anterior portion of the jugal area. In general the raised structure is similar to that of *Glyptochiton* de Koninck, 1883, from the Lower Carboniferous of Belgium and the United Kingdom but differs in position on the plates and the shape of the plates of the latter is different. The complete size and shape of the plates of *Plasiochiton curiosus* cannot be determined without destroying a portion of the specimen.

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